8

Special Features of Visibility Reduction in Flatfishes

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(Plates I-III)

Introduction

THE fishes of the order Heterosomata, the flatfishes, have many members which are remarkable for their ability to match closely the color of the background on which they rest and are evidently unique in their ability to match also the texture of the pattern of the background. Parker (1948), in noting this ability, wrote, "Responses to differences in pattern do not seem to have been observed in animals other than flatfishes; hence the exceptional nature of this group of teleosts." Mast (1916) published a series of plates in both black and white and color which clearly established the reality of this striking activity of the pigmentary system of flatfishes. Others, before and after him, who have contributed to our present understanding of background matching in this group of animals include Sumner (1910, 1911), Kuntz (1917), Schäfer (1921), Cunningham (1921), Hewer (1927, 1931), Meyer (1930, 1931) and Osborn (1939a, 1939b, 1939c, 1940, 1941a, 1941b).

These responses to background are exceedingly rapid and should not be confused with relatively permanent patterns which render a variety of other animals inconspicuous on some definite type of background. In the cases of the animals with a fixed pattern the disappearance is accomplished by the animal fitting itself against a suitable background and not by immediate and complex neural adjustments of the pigmentary system. A long list of forms which possess such comparatively stable patterns may be found in Cott (1940). These are widely distributed throughout the animal kingdom. Reports on various special cases of this type of behavior in fishes have been summarized by Atz (1951) and still others added by Uchida (1951). Obviously there is no sharp dividing line between animals which simply "melt" into the background and those which closely "mimic" some object, a division between such categories being often merely subjective.

There are, in addition to the problems of background matching, which have been studied by the workers mentioned above, other peculiarities in the pigmentary behavior of the Heterosomata. These, which include pigmentary behavior of the young and larval stages, have evidently never been studied nor related to the pigmentary behavior of the adults. Attention is herewith called to certain of these peculiarities and to some of the problems they pose in the Bothidae and the Achiridae.

Observations on Pigmentation and Behavior

The following data are based on original observations on pigmentary and other behavior of three species of the family Achiridae and one of the family Bothidae.

Patterns and Pigment in Achirids

Small individuals of *Trinectes lineatus* (Linnaeus)[1] of about 20 mm. in standard length are occasionally to be found near the laboratory and, so far, always in a solid black condition. One such individual, taken on January 15, 1952, was kept under continuous observation for more than five months in an aquarium provided with running sea water. This aquarium was floored with the typical light sand of the region, against which the fish was notably conspicuous. The fish at no time hid in corners of

[1] There has been considerable confusion in the nomenclature of these fishes. According to Chabanaud (1941), this form should be known as *Trinectes lineatus browni* (Günther), which see for a discussion of the matter.

the aquarium but regularly stationed itself on some centrally located portion of the aquarium bottom. Here it would lie, exposed on the very light sand, very often with no sand cover at all and seldom with more than a few grains. It was never seen to cover itself completely, a performance otherwise common in flatfishes. Some act disturbing the fish, such as pushing it about with a light rod, would not cause an alteration of this general behavior. It would usually move off slowly when the rod was thrust at it, with a peculiar form of locomotion resembling that of a large broad flatworm. It would so flute its marginal fins as to appear ruffled. Evidently the mechanics of this locomotion, which has been discussed in detail by Chabanaud (1941), is actually close to that of similarly-shaped flatworms. Once when so disturbed it shook off what few grains of sand were resting on it and rushed to nearly the exact center of the aquarium bottom, where it lay fully exposed and very conspicuous.

Lest it be thought that this was merely a melanistic individual which was unable to change its coloration at all, it may be pointed out that after dark the fish, discovered by flashlight, would always be found to be exhibiting the more usual cross bands (see Plate I, Figures 1 and 2).

Since most blinded fish in strong light develop their darkest phase, on which subject Parker (1948) gives a brief historic review, the presence of vision in this individual was carefully checked. This could be readily established by the accuracy of its striking at such things as *Artemia* as well as by the associated eye and body movements.

The above notes and photographs were made during January. By May the fish had altered its pigmentary behavior to the following. During the daytime it alternated between burying itself in the sand, so that it could only be seen partially or not at all, and exposing itself. At these latter times it came to show its former night time pattern with increasing frequency during the daylight periods. The coal-black phase appeared less and less often and usually the fish was a slate gray with black bars or dark brown bars. Sometimes it would swim about holding little piles of sand on various places on its flat body. The aquarium in which all this change transpired was near, but not directly, under a skylight. The significance of the resultant reduction of light intensity, as compared with the open harbor, is considered later.

Another sole, *Trinectes inscriptus* (Gosse), with a fairly inconspicuous pattern and color, always buried itself completely and with extreme rapidity, in the same sand. This action was so fast and with such immediate vigor that it was impossible to photograph the fish against a sand background. The photograph of this fish, Plate I, Figure 3, which appears to be that of the fish resting on the sand, was actually taken when an expedient was devised to circumvent the fish's rapid response. The fish was placed in a glass bowl which contained water only and then the bowl was placed on top of a pile of sand. The violent action of the fish in its fruitless attempts to bury itself was "stopped" photographically by using an electric photoflash. Although this fish, as may be noted from the photograph, is not exactly conspicuous on the sand of the area it inhabits, it still does not nearly approach the better background matches so usual in these fishes. As far as could be determined from aquarium observations, this fish was completely nocturnal.

On the west coast of Florida, at the Palmetto Key Laboratory of the old New York Aquarium, in 1940, eggs of *Trinectes lineatus* collected by tow net were carried through metamorphosis in finger bowls. At the time when the one eye began its migration to the other side of the head, general pigmentation was well advanced so that the fish was fully pigmented before the transformation was completed. This fish, as the eye migrated and the pigmentation increased, behaved in a manner suggesting that this period of change in the relationships of the visual fields was one of considerable behavioral difficulty. At first it swam at an angle as though attempting to retain a horizontal axis between the eyes. After this there followed a period, as the eye came over the dorsal profile of the head, in which the fish would lie down briefly, then get up and swim about erratically and then lie down again. Finally these periods of reclining became longer and longer, until the fish began to behave in a typically flounder fashion, the wandering eye, meanwhile, attaining the other side of the head. The water at this place is very turbid because of the presence of an extremely rich plankton, a condition which, as will be developed, has a distinct bearing on these pigmentary matters. Pigmentation appears in this form before the egg is hatched and Plate I, Figure 4, shows its extent five days after hatching, but long before any evidence of transformation appeared. The developmental stages of this species have been figured by Hildebrand & Cable (1938)[2] and the present material is in complete agreement with their illustrations.

Transparent and Pigmented Bothids

Small planktonic and fully glass-like individ-

[2] The same species in the usage of Chabanaud (1941).

uals of *Platophrys ocellatus* (Agassiz) may be taken about submerged lights in Bimini harbor with some degree of regularity. They are in an advanced stage, with the eyes on one side, and generally are found floating passively just under the surface of the sea. When placed in a bowl or aquarium they promptly settle to the bottom. Four views of such an individual are given in Plate II, two by transmitted light and two against a dark background. Oblique light was used in all but the first in order to take maximum advantage of the structural interference with light. It will be noted that the eyes are fully pigmented, the photographs with the dark background showing that the color of the investing tissues produces a light eyeball. This is a near cream color and very close to that of the light sand of this region.

In this stage these fish are extremely interesting to watch through a low power binocular. Mostly they rest quietly and show much oculomotor activity. Their extremely mobile and, of course, independently moving eyes, are capable of looking straight up. It is almost startling to have one such eye appear suddenly to be looking back at one through the other end of the microscope. That this great ocular activity is utilitarian is indicated by the fact that nearly always some particle is clearly in the line of fixation. That this really is the case may be demonstrated by the introduction of a quantity of newly hatched *Artemia.* The near ones become the objects of fixation just a moment before a small darting movement and engulfment of these food objects takes place. Because of the fish's great transparency, the swallowing of the *Artemia* may be easily followed to where it quickly lodges in the stomach. As the stomach becomes packed with *Artemia* and they die and are acted on by digestive juices they become a pale "boiled shrimp" pink which beautifully outlines the stomach. As the stomach does its work, small boluses of this material are seen to tear away from the main mass as the pyloric sphincter opens to pass the food along into the intestine. The whole process of digestion may be followed in this manner as though viewed on the screen of a fluoroscope.

If these fish are permitted to live under such conditions but with the normal sand background they nearly completely disappear, only the pigmented eyes being recognizable but, even so, extremely inconspicuous. Plate III, Figure 1, shows such a situation. The eyes may be seen as indicated but the mottling about them consists of the sand grains seen through the body of the fish. When this photograph was taken a few pigment spots had appeared, but earlier even these were not to be found. The fish may continue to live in this condition for a protracted time, not changing in pigmentation as rapidly as do many other planktonic larval fishes when brought in contact with a shore-like environment in an aquarium. These two fishes were taken about a submerged light on November 22, 1953. The photographs of one of them in Plate II, as noted in the legend, were taken on Nov. 23, 24, 26 and 27 respectively. Figure 1 of Plate III, which includes the two fish, was taken on Dec. 12, twenty days after they had been living in a sand-floored finger bowl. Two days later the next photograph, Plate III, Figure 2, was taken with the condition practically unchanged. Finally on December 19, after 27 days in the bowl (Plate III, Figure 3) the larger individual was seen to be fully pigmented and the smaller nearly so. In both the transparent and pigmented states and in the intermediate conditions these fish seem to be just about equally invisible. At this time it was necessary to abandon this series of observations, but these examples were carried to a point where the essential pattern of the adult had established itself. It may be noted that in all the fishes shown in Plate III, there is a small dark median spot about two-thirds of the distance from the eyes to the caudal peduncle. This made its appearance between the time the first of these pictures was made and the last of Plate II.

Discussion

From the foregoing descriptions it is evident that all flatfish pigmentary behavior is not uniformly a matter of matching the color and texture of the background. The following tabulation indicates the situations involving pigmentary and other behavior with regard to various environmental conditions which have been herein described.

Pigmentary Condition	Location of Fish	Light
	Trinectes lineatus	
Uniformly black	Exposed	Intense
Barred	Exposed	None
Barred	Exposed Buried	Moderate
	Trinectes inscriptus	
Reticulated	Buried	Intense or Moderate
Reticulated	Exposed	None
	Platophrys ocellatus	
Transparent	Exposed	Moderate
Background matching	Exposed	Moderate

The normal habitat of all was one of light sand, extremely clear water and extremely bright sunlight, excepting that of the Floridian

Trinectes. These reactions, which at first might seem to be merely fortuitous and without any regularity, can in fact be readily interpreted and understood in the light of the known behavior of teleost pigmentary systems. The explanations covering the situation in each of the four species examined follow.

The case of the Bahaman *Trinectes*, black on a light sand background, is completely explained on the same basis as the similar behavior of *Chaetodipterus* discussed at length by Breder & Rasquin (1955). As they indicate, in a fish responding to both light intensity and albedo under conditions of intense light and very light background, the melanophores will show maximal dispersal and the fish become substantially black. In very low light or none, as at night, what basic pattern is present but hidden reappears. Therefore there is no necessity to attempt to ascribe some biological utility to the seemingly pointless matter of "displaying" a pattern when it cannot be seen. After this fish had been kept in a laboratory aquarium for a long time it evidently reduced its amount of melanin in response to the lesser light intensity and showed its pattern in the daytime.

Trinectes inscriptus, which showed no evident pigmentary responses, simply remained nocturnal, with a pattern which was neither strongly contrasting with the background nor closely matching it.

Trinectes lineatus, living in a place of relatively low light and high albedo, showed both good matching and burying habits and had well pigmented larvae.

The glass-like planktonic young *Platophrys ocellatus* may settle to the bottom in that condition and so remain for some time and then gradually develop the extremely accurate bottom matching behavior so characteristic of the group.

One of the most interesting matters that developed in connection with the contemplation of these fishes was that their behavior, in each case, was appropriate to their pigmentation. The transparent, the closely bottom matching and the strongly bottom contrasting fishes all exposed themselves and each, in its way, thereby became less visible. Only those which were neither extremely contrasting nor extremely well matched to the bottom, hid or buried themselves. Note especially that the Bahaman *Trinectes*, at first so extremely black and "bold," became barred after a sojourn of some months in the less intense light of the laboratory, and changed its behavior appropriately. These clear changes in behavior in accordance with pigmentary differences add emphasis to the observations that fishes may employ either an extremely well matching pigmentation or a violently contrasting one to disappear effectively. That there are other fishes which darken on a light background in a strong light and thereby become inconspicuous was recognized by Breder (1948, 1949) and by Breder & Rasquin (1950, 1955).

The *Trinectes* taken from turbid water with a comparatively dark bottom was kept in a light colored bowl in the laboratory. It regularly lightened at night and darkened in the daytime. Here it seemed to respond chiefly to light intensity in a manner comparable to that of clear water *Trinectes* but less vigorously under the lesser stimulus. This followed from the extremely shallow water in the light bowl being insufficiently turbid to produce an albedo of large value, such as was normal to the environment.

In the case of the transparent *Platophrys*, as a purely practical matter it would seem to make little difference whether these fish remained transparent so that the bottom could be seen through them or whether they developed a very complicated pigmentary system which resembles the bottom under them as much as possible. The reasons for this change from the transparent to the pigmented, both of which evidently have equivalent value to the possessor, is probably to be found elsewhere. There may be two chief reasons for this change. It is conceivable that it would be difficult to prevent the development of pigment in the bright environment in which they live. It may be impossible for any large fish to remain transparent in such places, which circumstance would in effect relegate this device to application by only small organisms and for periods of relatively short duration. It also may not be very practical behavior to display the physiology of digestion through transparent sides on a sufficiently large scale. This demonstrated digestive activity might very well be attractive to the numerous marauding crabs of the region. Aside from these possibilities, there may be purely physical obstacles to the maintenance of transparency for long in such an environment. That is, some of the radiation may be physically injurious to certain tissues if long continued. It is thought, at least, that the comparatively subdued light of the laboratory made it possible for these fishes to retain their transparency longer than they could have in the wild state. The fact that *Platophrys* showed no change in general behavior, in passing from its transparent to its closely matching pigmentary pattern, would seem to indicate that the fishes were equally "secure" at all times during the transition.

In a more general consideration of teleost pigmentary reactions, reference may be made to some earlier studies of such matters. Breder (1949) found it convenient to prepare a table which listed the conceivably useful reactions a fish might find it possible to make in response to various stimuli. Pigmentary response was only one of the items listed and only that part of it which refers to reactions to background pertains to the present considerations. This fragment of the tabulation may be rephrased for present purposes as follows.

Possible pigmentary reactions in reference to background:

- A. Matching background
  - a. In general tone
  - b. In pattern detail
- B. Opposing background
- C. Indifferent to background

The data presented here show the fishes to subscribe to the items in this tabulation as below.

Trinectes lineatus	B., A., a.
Trinectes inscriptus	C.
Platophrys ocellatus—Transparent	C.
—Pigmented	A., b.

It is thus evident that each of the categories listed is represented in various ways by these fishes. The transparent *Platophrys* is considered "indifferent to background" in that it does not respond, not having any chromatophores with which to respond. *Trinectes inscriptus,* in the same category, is pigmented but there are no prompt pigmentary reactions. Each of the categories, as represented by these fishes, is primarily appropriate for the "freezing" type of organism, except that shown by *Trinectes inscriptus,* as an example of "C." This is the only fish which showed violent burying attempts. It is to be noted in this connection that *Trinectes lineatus* showed pronounced burying attempts only after it passed from its extreme background contrasting condition.

As a matter of general observation involving such species as *Pseudopleuronectes americanus* (Walbaum) and *Paralichthys dentatus* (Linnaeus), both excellent bottom matchers, the following conditions seem to obtain. They may be found either exposed and bottom matching or partially or fully buried with only their eyes above the sand. If pursued in shallow water over a uniform bottom they are not likely to bury themselves unless the pursuit is very vigorous. However, if they are driven onto a differently colored or textured bottom they are almost certain to bury themselves. This is, of course, in keeping with the data herein presented. Evidently the burying behavior supplements the pigmentary behavior in accordance with the requirements of the moment. This inter-relation of locomotor and pigmentary response to background has been shown, in a different guise, to be present in such simple background-matching fishes as *Gambusia,* by Breder (1947), and in *Cyprinodon,* by Breder & Rasquin (1951). In both cases the activity of the fishes was found to greatly alter when they passed over a nonmatching background. Also related to this is the reluctance of many fishes to move over a background toned differently from the one on which they have been swimming for some time, a matter discussed in the references above.

Some of the features associated with the development of glass-like transparency, common to the planktonic young of many fishes, have evidently not been previously discussed. Since various details of the present data suggest some of the necessary concomitants of a practically invisible body, they are discussed below.

It is noteworthy that in all the innumerable fishes that have such transparent early stages the eye is well pigmented. This is, of course, essential to image formation on the retina, and hence to vision. Evidently not one known fish has developed transparent but sightless eyes. Such a development would clearly extend the transparency to practical perfection. From the fact that this has not been done, it is deduced that vision plays such an important role in the lives of these fishes as to forbid its abrogation in the interest of perfection of transparency as a protective mechanism. There would thus seem to be a balance between the two conditions, in which the value of the retention of vision overrides the significance of cues which a predator might find from the presence of two "disembodied" black spots moving along a fixed distance apart. As an item of interest bearing on the above, very often, on examining a bucket or bowl of plankton, the first knowledge that the viewer has of the presence of the more extremely transparent fishes is just this indication of paired black dots moving along together without any apparent reason. This is, of course, a sophisticated recognition which the uninitiate do not usually make. If predators on these fishes are able to use similar means of detection it is evidently not sufficiently important to detract seriously from the survival value of combined transparency and vision.

Considerations of the relationship between the transparent fishes and the opaque ones follow. It would appear that certain limited tissues, such as muscle, cartilage and connective tissue, may be rendered completely transparent while others, by their very nature, cannot. The latter type includes at least erythrocytes with their contained haemoglobin. In the transparent fishes such unavoidably colored tissues are evidently kept at a minimum. Rasquin (in press), for example, in discussing the leptocephalus of *Albula*, shows that the red blood cells are remarkably few. With such structures kept at the minimum and dispersed in the animal, its visual density at macroscopic levels may be no greater than that of the surrounding water. To attain this condition the opaque tissues would have to be dispersed in the body of the animal in a manner approximately equivalent to the dispersion of particles suspended in the water and of their order of magnitude.

In a similar sense, pigmented fishes, both background matching and background contrasting, may disappear by mingling with particles of detritus which are of their own order of corporal magnitude. As found in a state of nature in water, most bodies either float or sink. Because of this, such association with particles about the size of the fishes in question is practically absent from mid-water but such hiding at the surface or on the bottom is common and widespread.

The next step in such a series by a single fish is the matching of a large number of smaller particles or objects. This evidently is done by the animals which closely resemble an area of background with which they are associated. This frees them from the need of having something sufficiently like themselves in size with which to mingle. There is no better illustration than a flounder matching a pebble background.

These observations lead to a general consideration of fishes living in extremely clear and brightly lighted water where optical cues are probably dominant or at least have much greater range and importance than in turbid water. That the interplay of the three most prominent methods of reducing conspicuousness, i.e., transparency, background matching and background contrasting, is most evident in brightly lighted clear water, should be expected. Likewise it should be expected that these features would be relatively reduced in turbid waters. The turbidity itself sharply restricts the range of vision while the increase in albedo which it induces, eliminates or restricts to very shallow water the background contrasting behavior. The data presented herewith and the pertinent references support such a correlation of light intensity and albedo with the locomotor activity and pigmentary behavior of fishes in reference to background. In a broader sense it would seem that these features of the behavior of the pigmentary system, together with the interacting nervous and endocrine systems, must have a very influential bearing on the evolution of pattern in fishes.

Summary

1. An entirely black *Trinectes lineatus* (Linnaeus) positioned itself conspicuously on a light sand background and showed a pattern of light cross bars only when the light intensity fell to a value too low for the human eye to see.

2. A *Trinectes inscriptus* (Gosse), with a network of fine lines, which was not notably conspicuously nocturnal, remained buried completely out of sight in the daytime.

3. An as yet untransformed *Trinectes lineatus*, taken in a tow net, developed pigment as its eye migrated and by the time this was complete the fish was fully pigmented.

4. Completely transparent and glass-like planktonic post-larvae of *Platophrys ocellatus* (Agassiz), with the eye transformation completed, on taking up residence on the same light sand did not develop pigment for a long time but nevertheless were practically invisible because of their glass-like transparency, but later when they did develop typical flounder background-matching color and pattern were just about as hard to find.

5. These apparently unorthodox pigmentary behavior patterns are discussed in reference to more usual modes and are found to be simply special or limiting cases, fully referable to known reactions and influences in the general behavior of teleost pigmentary systems.

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EXPLANATION OF THE PLATES

PLATE I. *Trinectes*

FIG. 1. *T. lineatus* (Linnaeus) in a typical pose and coloration on light sand in daylight. × 1½.

FIG. 2. The same fish in darkness. Picture made by means of prearranged photo-flash.

FIG. 3. *T. inscriptus* (Gosse) as seen against a background of the native sand in a pose never permitted by the fish under normal circumstances. × ⅔.

FIG. 4. *T. lineatus* before metamorphosis, showing the early development of extensive pigmentation, five days after hatching at a length of 2.5 mm.

PLATE II. *Platophrys ocellatus* (Agassiz)

FIG. 1. An individual in the extremely transparent stage seen against a dark background with reflected light, showing the light pigmentation of the eyes and some very pale chromatophores. November 23, one day after capture.

FIG. 2. The same fish against a dark background with extremely oblique reflected light. November 24.

FIG. 3. The same fish by transmitted oblique light, partially against a dark background, showing the glass-like transparency. November 26. × 3½.

FIG. 4. The same fish by transmitted light so arranged as to bring out the pale chromatophores shown in Figure 1. Here they show as mere small smudges. November 27. Photographs by Carol Mosher.

PLATE III. *Platophrys ocellatus* (Agassiz)

FIG. 1. The fish of Plate II and another larger individual against a background of light sand. This is the background normal to these fishes and on which they virtually disappear. They are here nearly transparent and the sand under them is plainly visible. The eyes of the smaller one can be found at the right of the picture, the fish facing up. Those of the larger are at the left, the fish facing down. December 12. × 1¾.

FIG. 2. The same fish. They are in the central portion of the picture. The smaller, to the right, is facing left, and the larger, to the left, is facing the lower left-hand corner. Slightly more pigment is present. December 14.

FIG. 3. The same fish, the larger showing full pigmentation and the smaller partial pigmentation. The smaller fish is to the left and facing a little to the right. The larger is to the right and facing a little left of upward. December 19. Photographs by Carol Mosher.